A Taxonomic Analysis of Pseudemyd Turtles (Testudines: Emydidae) from the New River, and Phenetic Relationships in the Subgenus *Pseudemys*

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ABSTRACT.— The morphology and geographical origin of a disjunct population of aquatic turtles, genus *Pseudemys (= Chrysemys* auct.) in the New River of Virginia and West Virginia are analyzed. Previous identification of these turtles as *"Chrysemys"floridana* is reappraised by comparison of shell proportions, color patterns, and cranial morphology to those of other species and subspecies of *Pseudemys (sensu stricto).* Discriminant analysis of 28 cranial characters broadly separates redbelly turtles *(P. rubriventris, P. nelsoni, P. alabamensis)* from New River *Pseudemys* and most populations of *P. concinna* and *P. floridana.* Based on morphological similarities, New River *Pseudemys* are identified as eastern river cooters, *P. c. concinna.* Natural history information and recent extensions of the known range suggest that *Pseudemys* in the New River represents a natural, established population. A late Pleistocene dispersal of cooters from the Virginia-North Carolina Piedmont Plateau into the New River is proposed.

INTRODUCTION

Bayless (1972) reported a population of cooter turtles in the New River at Bluestone Reservoir, Summers County, West Virginia. This locality is in the southern part of the state where the New River, a Kanawha-Ohio River tributary, enters from Virginia (Fig. 1). He tentatively identified the turtles in Bluestone Reservoir as *"Chrysemys"floridana,* without assigning them to subspecies. This population is broadly disjunct from the range of cooters in the Mississippi and lower Ohio River valleys and is isolated by the Atlantic-Ohio divide from the nearest populations in the Virginia and North Carolina Piedmont Plateau (Fig. 1).

Despite a thorough analysis of key morphological characters, Bayless (1972) failed to clearly establish the taxonomic status and probable geographical origin of the New River *Pseudemys.* This was unavoidable due to the poorly understood systematic and distributional relationships between *Pseudemys floridana* (LeConte) and *Pseudemys concinna* (LeConte) in northern parts of their ranges (Crenshaw 1955; Minton 1972; Pritchard 1979; Martof et al. 1980). Further uncertainty developed when Bayless' voucher specimens at the National Museum of Natural History (USNM 192635-7) were reidentified in 1973 as redbelly turtles, *Pseudemys rubriventris* (LeConte) (Fran I. McCullough, pers.
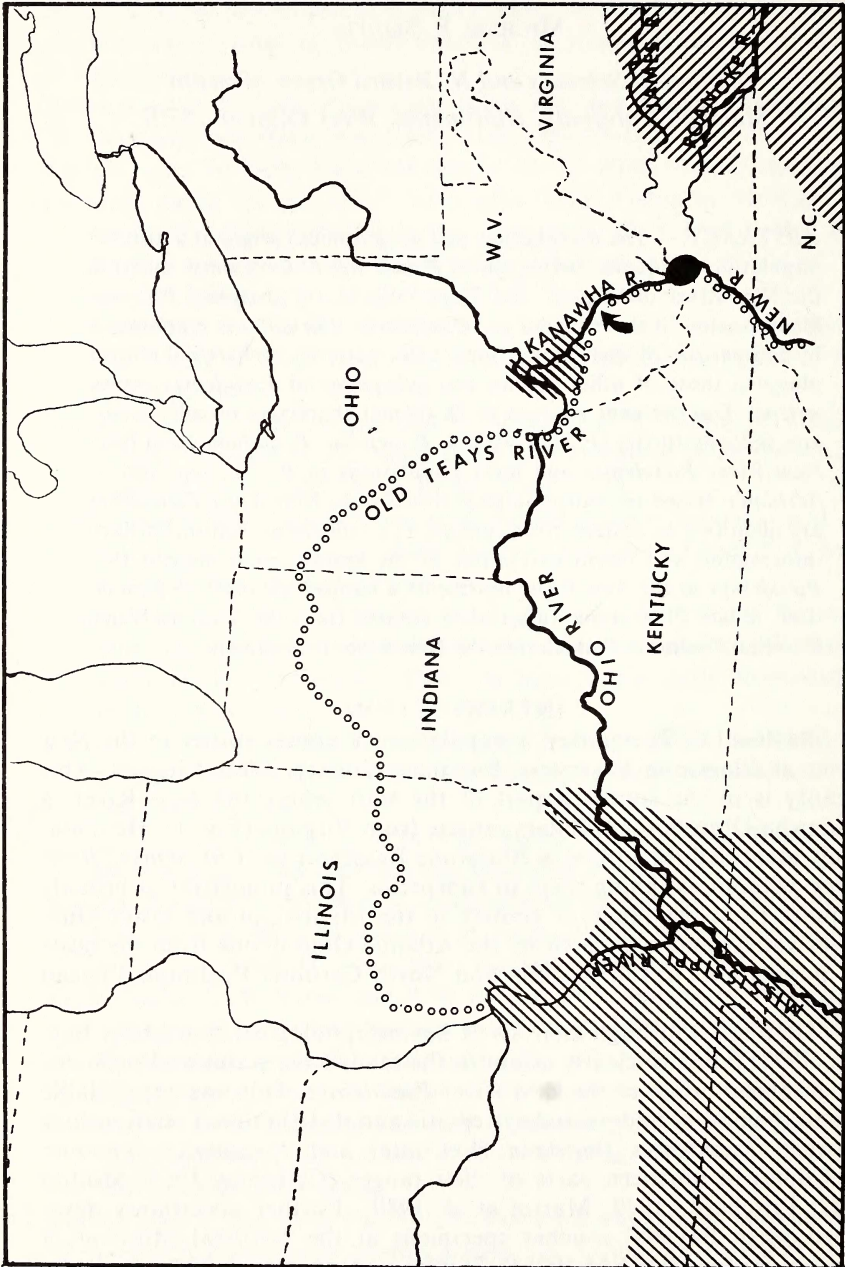
Fig. 1. Distribution of cooters in the upper Mississippi River Valley, Kanawha-Ohio River Valley, and Virginia and Carolina Piedmont. Dark oval indicates known range of *Pseudemys* in New River of Virginia and West Virginia. Location of Kanawha Falls indicated by arrow.

comm.). This species is known to occur only in drainage basins of the Atlantic slope (Conant 1975). Based on external morphology of the New River specimens, Carl H. Ernst (pers. comm.) suggested possible *P. rubriventris* influence in the population and the possibility of a *P. floridana* x *rubriventris* hybrid swarm similar to that reported in North Carolina by Crenshaw (1965). All that remained evident was that the turtles collected from the New River at Bluestone Reservoir belong to the subgenus *Pseudemys (sensu* McDowell 1964; Vogt and McCoy 1980). This subgenus includes *P. floridana, P. concinna* and a *P. rubriventris* series of *P. nelsoni* Carr, *P. alabamensis* Baur and *P. rubriventris.*

The present study, which analyzes cranial structure, shell morphology, color patterns and incidental natural history data, was designed to evaluate the taxonomic position and probable origin of *Pseudemys* in the New River. Although a systematic analysis of the subgenus *Pseudemys* was not the original or primary objective of the study, problematic levels of speciation and questionable validity of traditional key characters necessitated comparisons with all taxa in the subgenus, especially those with more northerly distributions.

MATERIALS AND METHODS

Twelve adult *Pseudemys* from the New River were examined and morphologically compared to other forms of the subgenus *Pseudemys.* The New River sample includes a specimen collected in Giles County, Virginia, in 1975; seven individuals collected in Bluestone Reservoir in May 1980; and the four specimens from Bluestone Reservoir described by Bayless (1972). Weaver and Rose (1967) found shell depth, nuchal (= cervical) scute underlap, and gular scute overlap especially useful in separating *P. floridana, P. concinna,* and *P. nelsoni.* These measurements were taken on New River *Pseudemys* and initially calculated as ratios following the methods of Weaver and Rose (1967) to allow direct comparison to their data. For subsequent shell comparisons among adult (153-300 mm carapace length) New River *Pseudemys, P. rubriventris,* and northern subspecies of *P. concinna* and *P. floridana* (Fig. 3): shell depth was calculated as a ratio of height to carapace length; gular scute overlap was calculated as 10X the ratio of gular scute length (dorsal surface) to plastron length; and nuchal scute underlap was calculated 10X the ratio of cervical scute length (ventral surface) to carapace length. Measurements were made with Helios or bow outside calipers. Characters traditionally used by Carr (1952) and Crenshaw (1955), such as patterns and coloration of head, neck, plastron and carapace, were also analyzed.

For phenetic analysis of adult cranial morphology, skulls from 4 Bluestone specimens were compared to skulls of 8 *P. rubriventris,* 4 *P. nelsoni,* 3 *P. alabamensis,* 5 *P. f. floridana,* 6 *P. f. peninsularis,* 13 *P. f. hoyi,* 5 *P. c. concinna,* 5 *P. c. suwanniensis,* 8 *P. c. hieroglyphica,* 9 *P. c.*

mobilensis and 6 *P. c. texana*. All specimens were adults and ranged from 27 to 57 mm skull length. Although the sex of some of the skulls examined was not identified, it was evident that none of the samples was skewed heavily toward males or females. Twenty-nine measurements were made on each cranium and mandible ($\pm$ 0.1mm): condylobasal length (midline length of skull, from posterior aspect of occipital condyle to anteriormost point of premaxillae); interquadratal width; supraoccipital length; pterygoid width (least); interpterygoid process width (greatest); orbital height and orbital width; narial height and width; prefrontal length (midline); interorbital width (least); postorbital length (width of postorbital arch, least distance from orbit to superior temporal fossa); postorbital-quadratojugal breadth (least distance between superior temporal fossa and ventral ridge of quadratojugal); jugal-quadratojugal length (least distance between orbit and tympanic cavity); maxillary alveolar width (least); foramen magnum width and height; basisphenoid-basioccipital length; interforamina stapedio-temporale width (distance between the temporal-stapedial foramina); anterior skull width (at anterior rim of tympanic cavity); posterior skull width (at posterior rim of tympanic cavity); intersquamosal breadth (distance between posterior aspects of squamosals); premaxillary height (midline); temporal arch width (least distance between rim of tympanic cavity and superior temporal fossa); otic capsule length (from posterior rim of tympanic cavity); dentary-coronoid height; dentary breadth (midline); dentary alveolar width (lateral); and lingual alveolar width (proximal to median ridge of dentary).

Due to intra- and interspecific size variation, regression analysis was applied to all skull measurements to remove linearly-related effects of size. Condylobasal length was used as the independent variable for regression analysis of the other variables. The SAS General Linear Models procedure produced residual values for each character; these values were used as "size-free" variables. Using these 28 variables, the SAS discriminant analysis procedure tested for homogeneity of within-group covariance matrices. As the 28 characters measured showed no evidence of heterogeneity of the within-group covariance matrices, groups (taxa) were compared by step-wise discriminant analysis using the computer program, BMD07M (Dixon 1974), which generates canonical variates with maximum between-group variance relative to within-group variance. The canonical variate means are plotted on the first two axes, and analysis of variance describes significant differences between groups ($P < 0.05$). Using canonical functions, the posterior probability of each turtle belonging to its respective group is computed and classified accordingly.

ABBREVIATIONS

ACE, United States Army Corps of Engineers, Huntington District.

AMNH, American Museum of Natural History.

CM, Carnegie Museum of Natural History.

FMNH, Field Museum of Natural History.

KU, University of Kansas Museum of Natural History.

MCZ, Museum of Comparative Zoology, Harvard University.

MES, Collection of Michael E. Seidel.

NCSM, North Carolina State Museum of Natural History.

UMMZ, University of Michigan Museum of Zoology.

USNM, National Museum of Natural History.

WVBS, West Virginia Biological Survey, Marshall University.

SPECIMENS EXAMINED

P. alabamensis: MCZ 1659-61, 1663, 1898; AMNH 107676. *P. nelsoni:* UMMZ 127059-60; AMNH 75640; MCZ 54131, 54684. *P. rubriventris:* AMNH 71276, 71280, 71282, 71293, 76175, 79132, 79134, 80218, 81869, 90641-42, 90644; CM 34409, 37272, 39672, 45188; FMNH 22137; MCZ 1666, 1671, 1674, 1677, 12877, 76679, 157828; MES 132. *P. f. floridana:* FMNH 8222; MCZ 1635, 1651, 46221-22; USNM 25260; AMNH 50985, 75641; NCSM 5884-85, 5927-28, 5930, 8518. *P. f. peninsularis:* FMNH 22074; UMMZ 12937, 130081, 44976; AMNH 64156, 69899, 110189; MCZ 19179. *P. f. hoyi:* KU 1176-79, 1185, 2221, 2800, 2830-31, 40166; MCZ 29080-81. *P. c. concinna:* USNM 8920, 15990, 60895, 92529-31; FMNH 22138; MCZ 1642, 1664, 12764, 54680; AMNH 75649; NCSM 10328, 17339, 20128, 20240, 20253. *P. c. suwanniensis:* UMMZ 127058, 129385; AMNH 80233; FMNH 22473; MCZ 43030, 54675, 54679. *P. c. mobilensis:* AMNH 69908; MCZ 1636-39, 1648-50, 1652, 42327. *P. c. hieroglyphica:* USNM 9659, 79449, 86728, 102679, 104397; CM 60560; CM (field series) 38068-69, 38071-72, 38077, 38107, 38132, 38134, 38155; UMMZ 101754, 128176, 133845; AMNH 69901-02, 69905-06; WVBS 3155, 3965. *P. c. texana:* USNM 26424, 26438, 78518; UMMZ 133836, 154982; MCZ 46483; KU 39986, 49630; AMNH 111960; MES 75. New River *Pseudemys:* USNM 192635-37; WVBS 4093; MES 489, 526, 528-29, 863, 865; UMMZ 88488; two adults released; two hatchlings MES uncataloged; shell bones ACE FS1-68, FS2-81, FS2-183.

RESULTS

Analysis of patterns and color in adult specimens from Bluestone Reservoir (Fig. 2) showed strong similarities to *P. concinna.* In all 12 specimens the submarginals contain dark markings that are usually open circles rather than the smudgelike or solid circles common in *P. rubriventris* and *P. floridana* (Carr 1952; Mount 1975). In most individuals the bridge has an extensive dark pattern that contacts the submarginal markings. The pleurals have relatively thin yellow-tan lines and some individuals show the clearly defined "C" figure on pleural II typical of *P. concinna.* Ventral and supratemporal stripes on the head and
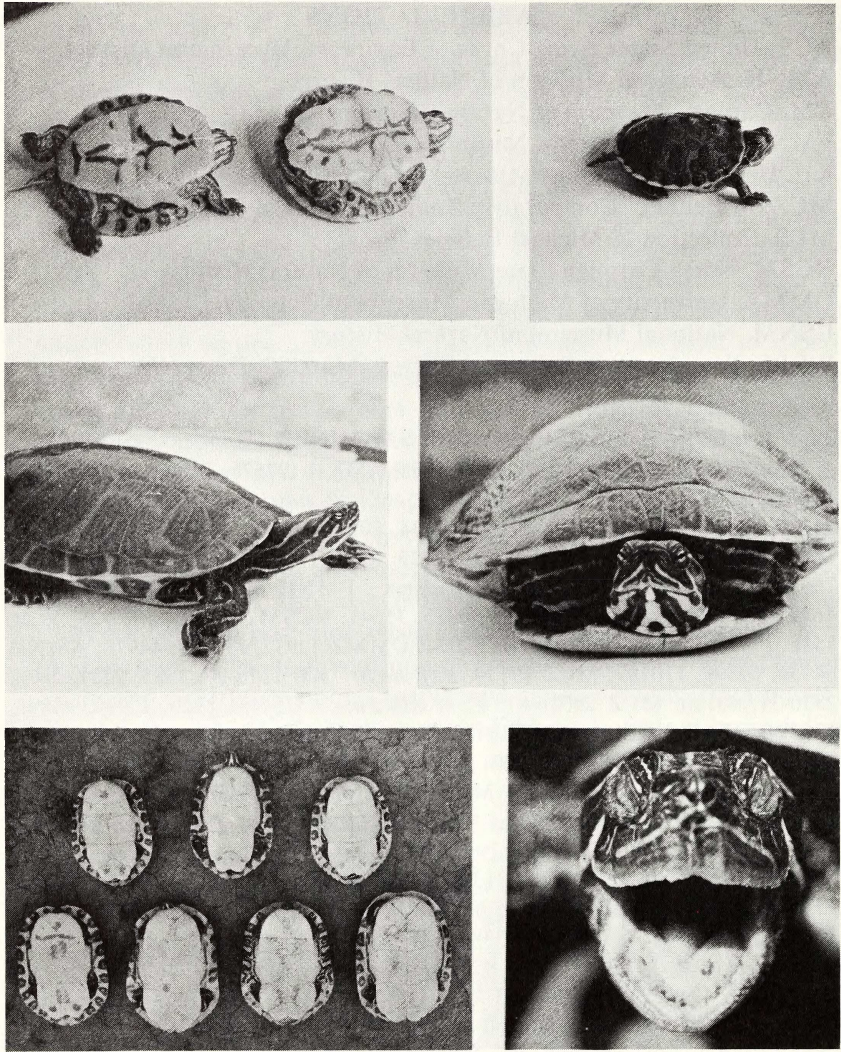
Fig. 2. Ventral and dorsal views of hatchling (above) and adult (middle and below) *Pseudemys* from Bluestone Reservoir, Summers County, West Virginia.
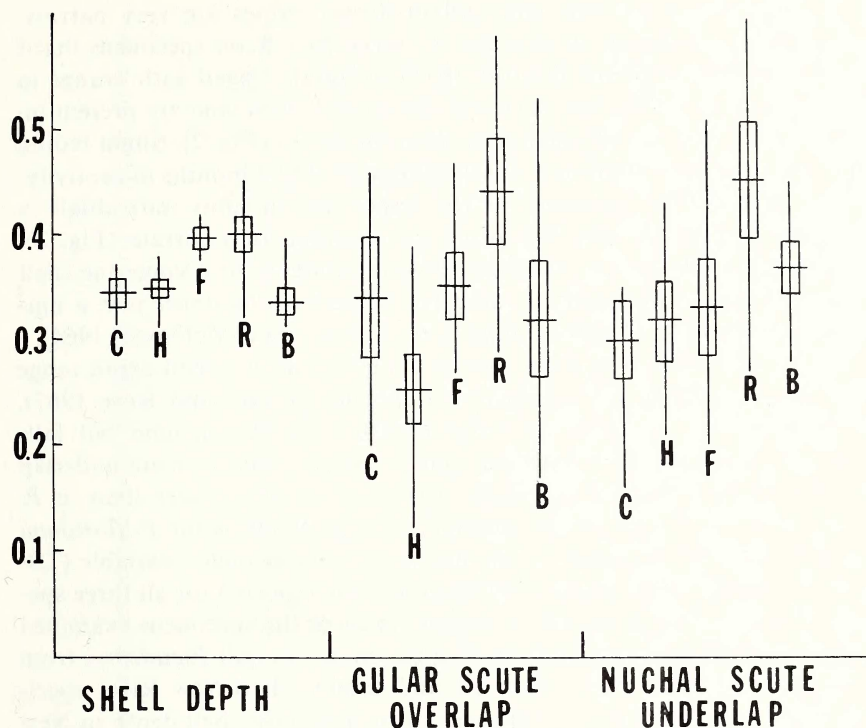
Fig. 3. Measurements of 7 *P. c. concinna* (C) from Virginia and North Carolina; 11 *P. c. hieroglyphica* (H) from Indiana and Tennessee; 8 *P. f. floridana* (F) from North Carolina, South Carolina and Georgia; 14 *P. rubriventris* (R) from Massachusetts, New Jersey, Pennsylvania, Delaware, Virginia and North Carolina; 12 *Pseudemys* (B) from New River, Virginia and West Virginia. Horizontal lines are means, vertical lines are ranges, rectangles are one standard deviation. Values are ratio calculations described in MATERIALS AND METHODS.

neck are broad whereas paramedian dorsal stripes are very narrow, sometimes convergent or obscure. All seven New River specimens that I collected have a yellow plastron that was lightly tinged with orange in two individuals. Plastral markings typical of *P. concinna* are present on each turtle, but less prominent in older specimens (Fig. 2). Slight fading of markings and coloration was evident after 2 to 3 months in captivity. The cutting edge (tomium) of the upper jaw in most individuals is weakly emarginate and the lower jaw is moderately serrate (Fig. 2). Four skulls which were analyzed show no evidence of a vomerine shelf contributing to the crushing (alveolar) surface of the upper jaw, a unique characteristic of species in the *rubriventris* series (McDowell 1964).

Twelve adult New River turtles examined have a shell depth range of 31.1 to 39.4 (ratio calculations following Weaver and Rose 1967), which broadly overlaps the range reported for *P. concinna* but falls below the ranges of *P. floridana* and *P. nelsoni*. Nuchal scute underlap ratios in New River *Pseudemys,* 16.0 to 23.4, are greater than in *P. concinna* but are within the combined range of ratios for *P. floridana* and *P. nelsoni*. The gular scute overlap ratio was highly variable (7.9-18.8), falling within the combined ratio range reported for all three species (Weaver and Rose 1967). Because most of the specimens examined by Weaver and Rose were from Florida, shells of adult *Pseudemys* from northern localities were measured and compared to New River specimens. These ratios (Fig. 3) again indicate a shallow shell depth in New River turtles (B) and *P. concinna* (C,H). Gular scute overlap and nuchal scute underlap are greater in *P. rubriventris* (R), than in New River specimens (B) and northern subspecies of *P. floridana* (F) and *P. concinna* (C,H). However, these two characters are highly variable and apparently not effective in separating *P. concinna* and *P. floridana* outside of Florida.

Results from the discriminant analysis of all *Pseudemys* skulls are presented in Figure 4. On the first canonical axis (K_1) plots of skulls in the *rubriventris* series (A,N,R) are clearly disjunct from all forms except *P. c. texana* (T). Broad separation is seen between *P. rubriventris* (R) and New River *Pseudemys* (B). Also noteworthy is the separation, on the second canonical axis (K_2) of *P. alabamensis* (A) from *P. rubriventris* (R) and *P. nelsoni* (N). The first two axes account for 51% and 12% of the total dispersion, respectively. In order of increasing importance, temporal arch width, jugal-quadratojugal length, interorbital width and dentary alveolar width were the most influential characters providing separation on the first axis (Table 1a). Anterior skull width, dentary alveolar width, and lingual alveolar width contributed most to separation on the second axis (Table 1a). All individuals were classified into their appropriate taxa, except one *P. c. mobilensis* that was placed in *P. f. floridana* and one *P. f. hoyi* that was placed in *P. c. hieroglyphica*. The *P. c. mobilensis* specimen (MCZ 1651) was collected within the

Table 1. Coefficients for the most influential morphological variables (measurements of cranium and mandible) in three discriminant analyses (a,b,c) of *Pseudemys*.

Variable	a		b		c	
	axis 1	axis 2	axis 1	axis 2	axis 1	axis 2
Narial height	—	—	—	—	-1.24	0.97
Interorbital width	-1.43	—	2.14	—	—	—
Jugal-quadratojugal length	-1.04	—	—	-2.11	—	—
Maxillary alveolar width	—	—	1.42	—	—	—
Foramen magnum width	—	—	—	—	1.19	—
Basisphenoid-basioccipital length	—	—	—	—	-0.97	—
Anterior skull width	—	0.98	1.64	—	—	—
Temporal arch width	0.99	—	—	1.67	—	—
Dentary alveolar width	1.59	-1.20	-2.76	—	—	0.61
Lingual alveolar width	—	1.51	—	2.55	-0.75	—
Prefrontal length	—	—	—	—	—	0.89

range of *P. f. floridana* (Mobile, Alabama) and a resemblance to *P. floridana* was noted prior to discriminant analysis. This skull was re-identified as *P. f. floridana* for subsequent comparison. The misclassification of a *P. f. hoyi* skull as *P. c. hieroglyphica* is not surprising considering the proximity of means (H,Y) for these forms (Fig. 4). This skull was reassigned to *P. c. hieroglyphica* in further analyses. Based on the 28 cranial characters measured, analysis of variance indicated significant differences comparing New River *Pseudemys* to all taxa ($P < 0.01$) except *P. c. concinna* ($P > 0.05$), *P. c. suwanniensis* (> 0.01), and *P. c. mobilensis* ($P > 0.01$).

To further analyze the relationships of New River *Pseudemys* to *P. floridana* and *P. concinna*, discriminant analysis of skulls was applied again, with the *rubriventris* series omitted. Results of this analysis are similar to the first, but three clusters now become apparent (Fig. 5): a western and Mississippi Valley group (*P. c. texana, P. f. hoyi, P. c. hieroglyphica;* TYH), an eastern *P. concinna* group (*P. c. suwanniensis, P. c. mobilensis, P. c. concinna,* and New River *Pseudemys;* SMCB), and an eastern *P. floridana* group (*P. f. floridana, P. f. peninsularis;* FP). Noteworthy is the broad separation (on the first axis, K_1) of *P. f. hoyi* from other *P. floridana* skulls and its extensive overlap with *P. concinna* (Fig. 5). The first two canonical axes account for 49% and 20% of the total dispersion, respectively. In order of increasing importance, maxillary alveolar width, anterior skull width, interorbital width and dentary alveolar width are the most influential characters providing separation on the first axis (Table 1b). Temporal arch width, jugal-quadratojugal length and lingual alveolar width contributed most to separation on the second axis (Table 1b). All individuals were classified into their assigned groups. Results from analysis of variance show New River skulls significantly different from all taxa ($P < 0.05$) except *P. c. concinna* and *P. c. suwanniensis* (canonical means enclosed by broken lines in Fig. 5).

A third discriminant analysis of skulls, with *P. f. floridana* and *P. f. peninsularis* removed, was applied to further clarify relationships with the races of *P. concinna* (Fig. 6). The first two canonical axes collectively account for 77% of the total dispersion. Characters most responsible for separation on the first two axes are presented in Table 1c. Results from this comparison indicate a very close phenetic relationship between the eastern river cooter, *P. c. concinna* (C) and New River *Pseudemys* (B) (Fig. 6).

Observations on reproduction of cooters recently collected from Bluestone Reservoir, discovery of a previously overlooked museum record, and examination of archeological material have also contributed to a better understanding of *Pseudemys* in the New River. Three adult females from Bluestone Reservoir, collected 15 May 1980 and X-rayed 7 June (following the method of Gibbons and Greene 1979) showed no
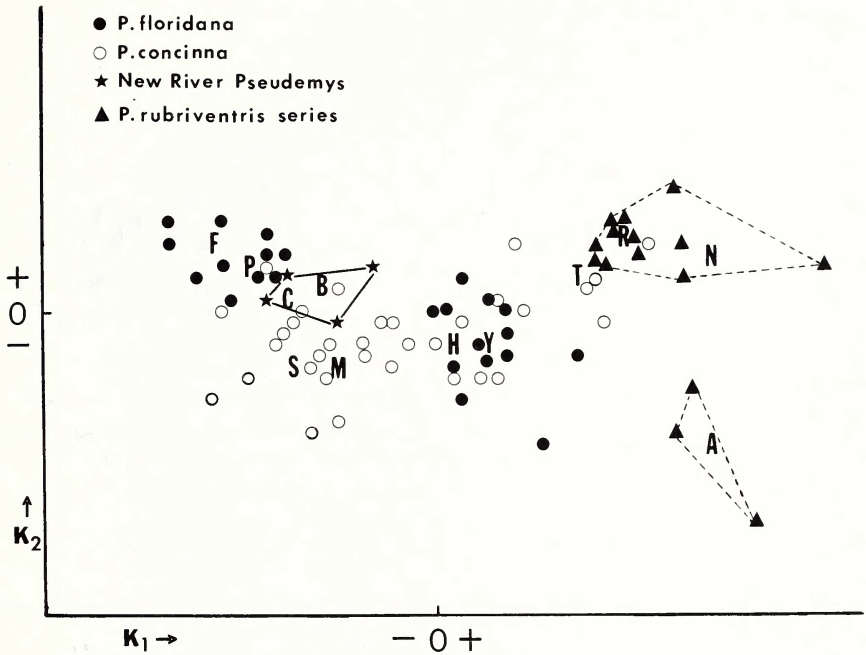
Fig. 4. Variates for skulls of the subgenus *Pseudemys* plotted on the first (K₁) and second (K₂) canonical axes. Individual skulls represented by symbols, and letters represent canonical variate means for *P. alabamensis* (A), New River *Pseudemys* (B), *P. c. concinna* (C), *P. f. floridana* (F), *P. c. hieroglyphica* (H), *P. c. mobilensis* (M), *P. nelsoni* (N), *P. f. peninsularis* (P), *P. rubriventris* (R), *P. c. suwanniensis* (S), *P. c. texana* (T), *P. f. hoyi* (Y). Values for New River *Pseudemys* connected by solid lines. Broken lines connect the most dispersed values for *P. rubriventris* and *P. nelsoni* collectively, and values for *P. alabamensis*.
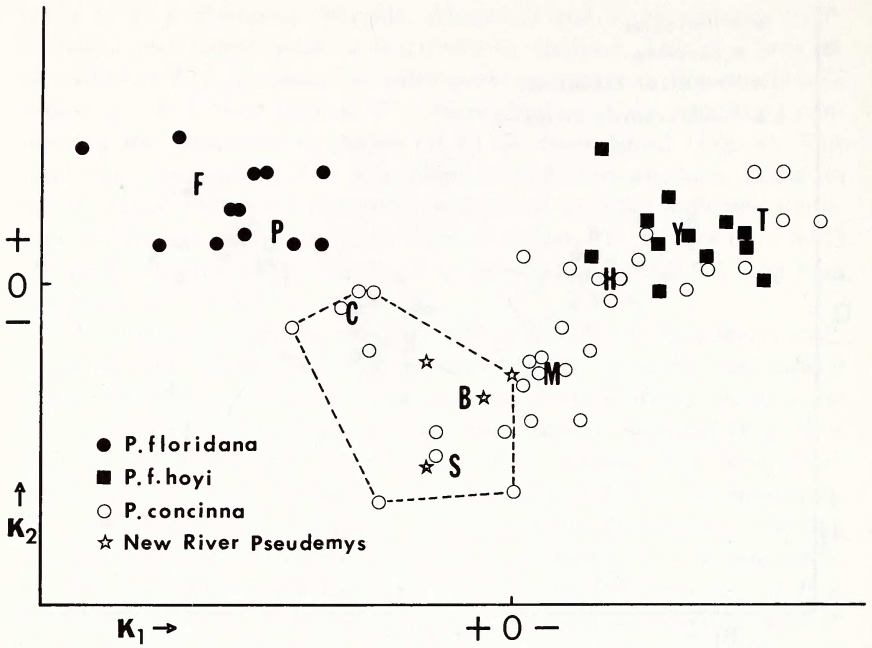
Fig. 5. Variates for skulls of *P. floridana* and *P. concinna* plotted on the first (K_1) and second (K_2) canonical axes. Individual skulls represented by symbols, and letters represent canonical variate means for New River *Pseudemys* (B), *P. c. concinna* (C), *P. f. floridana* (F), *P. c. hieroglyphica* (H), *P. c. mobilensis* (M), *P. f. peninsularis* (P), *P. c. suwanniensis* (S), *P. c. texana* (T), *P. f. hoyi* (Y). Broken lines connect and enclose New River skulls and plots for the subspecies *P. c. concinna* and *P. c. suwanniensis*, which show no significant difference (P > 0.05) from New River *Pseudemys*.
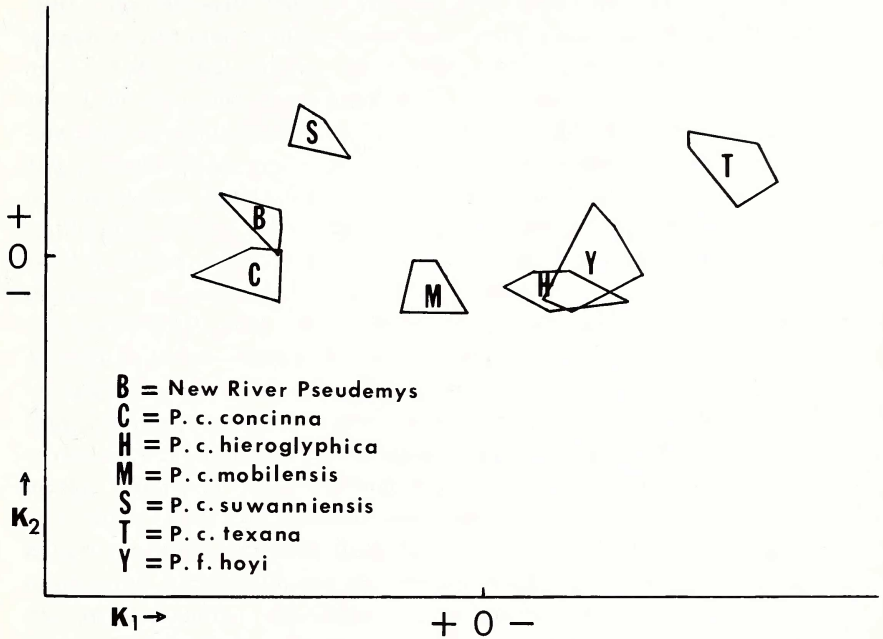
Fig. 6. Variates for skulls of *P. concinna* plotted on the first (K_1) and second (K_2) canonical axes. Lines connect the most dispersed values about canonical means, which are represented by letters.

evidence of ripe (shelled) eggs. One of these females, dissected on 9 July, contained no oviducal eggs. A second female held in laboratory deposited eight eggs 10-21 July, three of which were incubated at 30-35° C in moist vermiculite. Two hatched on 4 September and the third was apparently infertile. Unlike *P. rubriventris* the two hatchlings have yellow plastrons, and unlike *P. floridana* the plastrons are extensively patterned (Fig. 2). Dark markings also appear on the ventral surface of each marginal (submarginal) and throughout the bridge. These hatchlings and adults, maintained in laboratory and offered a wide variety of food for three months, were entirely herbivorous. A juvenile *P. concinna* (UMMZ 88488, fluid preserved), collected 3.2 km east of Hinton in the Greenbrier River (near its junction with the New River below Bluestone Reservoir), Summers County, West Virginia, has markings nearly identical to the Bluestone hatchlings. This fluid preserved specimen, presumably overlooked by other investigators, was taken in 1934 (collector unknown) and confirms the presence of cooters in the New River system prior to the construction of Bluestone. Dam, 1942-1949. Thus, the hypothesis presented by Bayless (1972) that the impoundment created new habitat necessary for establishment of an introduced population can be dismissed. Further evidence for a relatively long natural history of *Pseudemys* in the New River comes from examination of turtle bones recovered from an archeological site (46SU3, Fort Ancient Village 1100-1300 AD) at Bluestone Reservoir (Applegarth et al. 1978). A peripheral ACE FS2-81, pleural ACE FS2-183, and hypoplastron FS1-68 were identified as *Pseudemys* cf. *P. concinna* by Dale R. Jackson (pers. comm.).

DISCUSSION

The cooter species *P. concinna* and *P. floridana* have had a long, confused taxonomic history. Following LeConte's (1830) original descriptions, Carr (1935, 1952) considered *P. concinna* and *P. floridana* a conspecific assemblage of eight subspecies under *P. floridana.* However, Carr (1952) commented that at least the Florida races, *P. f. peninsularis* and *P. f. suwanniensis,* were broadly sympatric and behaved as separate biological species. Crenshaw (1955) partitioned the cooters, recognizing both *P. concinna* and *P. floridana.* A major weakness of Crenshaw's conclusion is that it was based primarily on relationships between Florida forms, without a thorough understanding of ecological and morphological relationships of populations elsewhere. Another criticism of Crenshaw's work is that it relied heavily on highly variable characters such as markings and pigmentation, which may show greater variation within a population than between species. These phenotypic characters may also be subject to strong environmental influence. Mount (1975) reported that the color of markings fades rapidly in captive *P. concinna* and concluded that pigmentation in cooters has little systematic value.

Moreover, Ewert (1979) demonstrated that, at least in map turtles of the genus *Graptemys,* diagnostic head markings may be altered by varying incubation temperatures and therefore are not entirely under genetic control. Nevertheless, the taxonomic arrangement of Crenshaw (1955), although never published with full supporting documentation, has generally been followed (Conant 1961, 1975; Ernst and Barbour 1972; Wermuth and Mertens 1961, 1977).

Fahey (1980) proposed that *P. concinna* once again be placed in the synonymy of *P. floridana,* a conclusion based exclusively on examination of turtles from Louisiana. Although Fahey's results suggest the presence of a single species in the restricted region of his study, they certainly do not substantiate relationships throughout the ranges of *P. floridana* and *P. concinna.* In addition to Fahey's report, there are numerous published references to either weak morphological separation or putative hybridization between *P. floridana* and *P. concinna* in the Mississippi Valley and areas to the west (Brown 1950; Smith 1961; Anderson 1965; Webb 1970; Barbour 1971; Minton 1972; Mount 1975). Traditional key characters, such as plastral markings and a "C" figure on the second pair of pleurals, which are used to distinguish *P. concinna* from *P. floridana,* are not consistent for central and western populations that are seemingly convergent in some characters. Ward (1980) found no cranial characters with which he could separate the midwestern subspecies *P. f. hoyi* and *P. c. hieroglyphica* and placed them in synonymy. My results from discriminant analysis of cranial morphology (Figs. 4, 5, and 6) support that decision. However, conclusions regarding conspecific status for all turtles assigned to *P. concinna* and *P. floridana,* especially eastern forms, must await a comprehensive and geographically broad analysis.

Based on shell markings and proportions, overall pigmentation, and cranial morphology, New River *Pseudemys* are clearly distinct from *P. rubriventris.* The emarginate tomial surface of New River specimens (Fig. 2) might be interpreted as a weakly developed notch bordered by cusps, characteristic of species in the *rubriventris* series (Carr 1952; Ernst and Barbour 1972). Weak cusps, however, have been reported in several populations of cooters allopatric and sympatric with redbelly turtles (Carr 1952; Crenshaw 1955; and personal examination of skulls: CM 60560, UMMZ 127058, MCZ 54680). Furthermore, prominent cusps are typical in *P. c. texana* (Ernst and Barbour 1972). Jackson (1978) cautioned that little taxonomic weight should be given to trophic structures in *Pseudemys.* The overall similarity in cranial morphology of *P. c. texana, P. nelsoni,* and *P. rubriventris* (Fig. 4) may represent convergence of character states resulting from similar feeding habits.

A shallow carapace with evidence in some individuals of a "C" on pleural II, and extensive dark markings on plastral, axillary and inguinal scutes, are characteristics of New River cooters that justify their

assignment to *P. concinna*. Further indication that these turtles are referrable to *P. concinna* comes from discriminant analysis of cranial morphology. Skulls of New River turtles are phenetically close to *P. c. concinna* and *P. c. suwanniensis,* and broadly separated from all forms of *P. floridana* (Fig. 5).

Recent evidence of fertile eggs, numerous sight records of basking adults, discovery of bones 700 to 800 years old, rediscovery of a museum specimen collected in 1934, and extensions of the known range 22 km south of Bluestone Reservoir to Giles County, Virginia and 2 km northeast of Bluestone Reservoir in the Greenbrier River, West Virginia, support the hypothesis that cooters in the New River represent a natural, established population. Assuming an origin not involving human interference, there are two possible avenues for dispersal that could have allowed *P. concinna* to enter the New River. The first is an early Pleistocene invasion from the Mississippi Valley (embayment region) through the old Teays River, which followed the course of the present Kanawha and New Rivers (Fig. 1). An argument for this route is supported by the occurrence of cooters referrable to the Mississippi Valley subspecies *P. c. hieroglyphica* in the lower Kanawha River, Mason County, and Mud River, Cabell County, West Virginia (Seidel and Green, in press). To examine this relationship, twelve New River specimens were compared to seven adult and two subadult *P. c. hieroglyphica* from Reelfoot Lake, Tennessee. New River *P. concinna* differ from these turtles in having: a lower carapace with the highest point at the middle; shell not usually constricted at the region of the sixth marginal; fewer concentric light lines on the carapace; dark markings on the bridge that frequently contact submarginal blotches; alveolar surface of lower jaw relatively narrow; and fewer and broader stripes on the head and neck, especially ventrally. These characteristics are more typical of the Piedmont subspecies, *P. c. concinna* (Carr 1952; Mount 1975). Although the New River is a Kanawha River tributary, it is separated from the Ohio and Mississippi River valleys (inhabited by *P. c. hieroglyphica*) by Kanawha Falls (Fig. 1). This falls is believed to be one of the largest natural river barriers east of the Rocky Mountains (Jenkins et al. 1971). Furthermore, rapids and cataracts in New River Gorge just above Kanawha Falls provide an effective barrier to fish distribution between the Kanawha and New Rivers (Hocutt et al. 1979). Therefore, preglacial dispersal of cooters from the Mississippi Valley into the upper Teays (New) River may not have been possible.

A second potential avenue for dispersal of *P. concinna* is over the Atlantic-Ohio divide of Virginia and North Carolina. Wright (1934), Thompson (1939), Dietrich (1959), and Ross (1969), reported late Pleistocene stream captures of the New River by the James and Roanoke, two rivers inhabited by *P. c. concinna* in the Piedmont (Martof et al. 1980; and Fig. 1). Comparisons of New River *P. concinna* to five adult,

fluid preserved *P. c. concinna* from the Piedmont of North Carolina indicate an overall greater similarity in markings and shell shape than seen comparing New River cooters to *P. c. hieroglyphica*. This relationship is also supported by cranial morphology. In Figures 4-6, New River specimens clearly plot closer to *P. c. concinna* than to *P. c. hieroglyphica*. Although the subspecies of river cooters are not well defined and their distinguishing characteristics are inconsistent within and between populations (Mount 1975; and pers. observ.), *Pseudemys* in the New River of Virginia and West Virginia are most similar morphologically to the eastern river cooter and are here assigned to *P. c. concinna*. Therefore, I suggest that during the Pleistocene, *P. c. concinna* ranged farther up Piedmont streams in Virginia and North Carolina and gained access to the New River through stream capture. The presence of the eastern painted turtle, *Chrysemys picta picta*, in the upper Tennessee (Ernst 1970) and New River systems offers additional evidence that this corridor has been used in the dispersal of aquatic turtles. *Chrysemys p. picta* is typically an Atlantic Slope subspecies that is replaced by the midland painted turtle, *C. p. marginata,* in the Ohio River system. Two specimens from Mercer County, West Virginia (WVBS 4238, 4415) and two specimens from Summers County, Bluestone Reservoir (MES 866, 868) are referrable to the eastern subspecies. Two additional specimens from Bluestone Reservoir (MES 867, 869) have characteristics typical of *C. p. picta* x *p. marginata* intergrades. River cooters are highly aquatic turtles and less likely than painted turtles to enter a new drainage by terrestrial migration (Ernst and Barbour 1972). However, the preference of *P. c. concinna* for rocky, fast-running stream habitats (LeConte 1836; Carr 1952; Pritchard 1979) might have facilitated its dispersal through small-stream captures.

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